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SALINITY TOLERANCE OF SOME MARINE BIVALVES
FROM INSHORE AND ESTUARINE ENVIRONMENTS
IN VIRGINIA WATERS ON THE WESTERN MID-ATLANTIC COAST!

М. Castagna and P. Chanley?

ABSTRACT

Many species of estuarine bivalves have a distribution pattern closely cor-related with salinity, indicating the importance of salinity in determining these patterns. The approximate salinity tolerance range for 36 species of bivalves. is described. Tolerance limits for 29 species were determined in laboratory experiments. Most of these species display a remarkable degree of euryhalinity. All survived a minimum salinity of at least 17.5% ап4 25 species survived at 12.5%. Twenty species survived at various lower salinities.
Salinity tolerance for a given species is not constant but varies with season, salinity experience, and temperature. Burrowing, feeding and reproduction usually occur at nearly all salinities at which survival is possible. Byssal formation requires a higher salinity than is necessary for other activities.
In Virginia about two-thirds of the species of salt-water bivalves discussed can be found over the entire salinity range they are capable of tolerating in the laboratory. Eleven species do not occur over their entire potential salinity range. Eight of the 11 species, Yoldia limatula, Mytilus edulis, Venericardia tridentata, Lucina multilineata, Dosinia discus, Abra aequalis, Mya arenaria, Martesia cuneiformis, are near the geographic limit of their range; their distribution locally may be limited primarily by the tactors that determine their geographic range. The distribution of 5 species, Argopecten irradians, Congeria leucophaeta, Macoma mitchelli, Donax variabilis
and Spisula solidissima, may be influenced by predation, competition, or special environmental requirements. Four of the 11 species, Congeria leucophaeta, Macoma mitchelli, Donax variabilis, Rangia cuneata, occur in specialized habitats with low
species diversity.

INTRODUCTION distributional patterns Бу graphically Temperature is usually considered the illustrating a variation in the relative most important ecological factor in- numbers of species found at various fluencing the distribution of animals
(Gunter, 1957). Within an estuarine sys-
tem, salinity is generally the more ob-
vious environmental factor (Pearse &
Gunter, 1957). Many species have a dis-
tribution pattern closely correlated with salinity, and often are categorized accord-ing to the salinities in which they are found (Wass, 1965; Menzel, 1964; Wells, 1961) or identified with certain as-semblages that characteristically occur in a given salinity range (Ladd, 1951; Parker, 1959). Pennak (1953) summarizes the importance of salinity in determining

salinities. Carriker (1967) reviewed the classification and distribution of organ-isms in an estuary.
The distribution of most adult bivalve mollusks may be especially influenced by salinity since the relative immobility of these animals usually precludes migration from adverse salinity conditions. The literature abounds with accounts of mass mortalities associated with abnormal salinity conditions (Baughman, 1947). However, because of the variable nature of the environment, it is frequently difficult to ascertain from field ob-

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servations the precise effect of salinity
on natural distribution. The ability of most
bivalves to adapt to transient conditions of
unfavorable salinities by physical exclusion
(closing of shell, retreat into burrows,
closing of burrows, etc.) rather than by physiological adaptation further confuses attempts to determine their salinity tolerance limits from distributions (Kinne, 1967). Finally, from observations on natural distribution, it is difficult to differentiate between the influence of salinity and several other physical and biological factors (Kinne, 1967). For exam-ple, the edible mussel (Mytilus edulis L.) is limited to high salinity oceanic waters in Virginia not by salinity but because the low-salinity bay and inshore waters reach lethal temperatures in the summer (Hutchins, 1947; Wells & Gray, 1960; Read, 1967). The distribution of other species (Mya arenaria L. and Crassostrea virginica Gmelin), although overtly associated with low salinities in certain areas, may in reality reflect the influence of predation or biological competition (Nichy & Menzel, 1962; Menzel, Hulings & Hathaway, 1958).
Although the bivalve mollusks соп-situte a sizable biomass of the benthic and planktonic (as larvae) communities and are important economically and ecologically, very few data are avail-able on the salinity tolerances of most species. Furthermore, available infor-mation is based primarily on field obser-vations.
We have undertaken a study to demon-strate more precisely the salinity toler-ance of many species of bivalves occurring in the study area and with this informa-tion determine the influence of salinity on natural distribution. This includes a review of literature, experimental work and a discussion to correlate and evaluate results.
The scope of these studies has been limited to the effects of salinity on bivalves from the inshore marine and estuarine environments of Virginia as listed by Wass (1965). Since it is our purpose to survey the salinity tolerances

of many species rather than to treat a few exhaustively, emphasis has been placed on the effects on activity and survival of adults. The influence of salinity on growth and reproduction and its possible effect on the distribution of a species has received only cursory treatment in our experimental work.

PROCEDURE, METHODS, AND MATERIALS

Collections were made from 24 inshore and estuarine sites (Fig. 1). Spisula solidis-sima collections were supplemented by specimens from a commercial dredge boat working off Point Pleasant, New Jersey, in depths of 50-100 feet. Most collections were made in estuarine areas, such as the James and York Rivers, or in small tidal creeks, such as Occohannock ог Pungoteague Creek. These creeks and rivers drain into the Chesapeake Bay, and are usually sand or sand-mud areas with little or no vegetation. Plants, when pre-sent, were predominantly Zostera or Zostera and Rupia together. Salinities were usually below 22%o.
The high salinity species were collected from ocean beaches on the barrier islands east of the Delmarva Peninsula (land mass forming the eastern boundary of Chesapeake Bay) or Нот the small bays, creeks, or lagoons between these barrier islands and the peninsula. These were high salinity areas (27-32%) with very turbid waters, peat or sand sub-strata on the beaches and usually soft mud or sand-mud in the bays and lagoons. Specific information on collection sites is shown in Table 2.
Salinity tolerances were determined experimentally for 29 species. A few species were not included because they could not be collected in suitable numbers for experimentation. No experimental work was attempted when salinity tolerances could be determined adequately from published accounts. Except where otherwise noted, geographical ranges are from Abbott (1954). Attempts were made to follow the experimental procedures outlined below, but because of the

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FIG. 1. Sites collected for species used in salinity tolerance experiments.

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uniqueness of each species, modifica-
tions were often necessary.
Experimental salinities ranged from
0-30% at intervals of 2.541%. At
the beginning of each experiment, a
group of 10 animals was placed directly in each salinity. The control was the group placed in the experimental salinity that most closely approximated the salinity from which the animals were collected. The control was maintained at the same salinity throughout the ex-periment.
After animals had adapted to ex-perimental salinities, as determined by survival, filtering?, burrowing or other activity, groups were transferred by steps to different salinities at а rate of 2.5+1% per 48 hours or on occasion per 24 hours in an attempt to further extend the salinity range. When the maximum salinity range was determined in this man-ner, surviving groups were transferred directly to either the opposite extreme salinity at which any had survived or to the control salinity to determine if they could adapt to greater salinity changes in the reverse direction.
Observations were made daily and con-sisted of counting survivors, removing and measuring length of dead animals, coun-ting those that had burrowed or attached by byssus, and observing the ability of animals to filter algae. Observations were also made of nest-building by Amygdalum papyria (Conrad) and reproduction by Gemma gemma (Totten). Animals were not considered dead unless they gaped and failed to respond to repeated tactile stimuli or were obviously putrescent. Ability to burrow was assumed if the animal was wholly or partly buried in a natural position. Burrowing animals were dug up weekly to determine continued ability to burrow. Ability to filter was noted by the clearing of algae from the water and by fecal deposition. Experimental animals were collected from many areas throughout the entire

year. Collection details are summarized in Table 1. Since smaller individuals were more active and adapted better to labora-tory life, the smallest specimens available were used. Sufficient animals were ob-tained so that 10 could be maintained in each experimental container. Whenever possible, experiments were repeated until at least 40 animals were exposed to each experimental salinity. Although repeat experiments with the same species often included different populations, or were conducted at different seasons of the year, experimental results involving one species have been combined. It was sometimes necessary to hold animals until there was a sufficient number for an experiment. They were held in water of the same salinity as the area in which they were collected. All weak, damaged or dying animals were discarded before starting an experiment. Experimental details are summarized in Table 2. In each experiment, animals were maintained in containers with 400 cc, 3 liters or 6 liters of standing water (depending on the size of the animals). Aeration was provided for those species that displayed poor survival in holding containers or preliminary experiments without it.
Experimental salinities were adjusted by diluting salt water from the laboratory sea water system with pond water from the irrigation pond at the Virginia Truck Experiment Station, Eastern Shore Branch, Painter. This source of fresh water was chosen because the volume of water needed precluded the use of distilled water and preliminary experiments indicated that tap water was unsatis-factory. The total salt content of the pond water was 80 ppm.
Water temperature was taken daily and the range for each experiment is given
in Table 2. No means of controlling
temperature were used. Since temperature
varied considerably, average range
was 7.4°C, no attempt has been made to
more precisely present mortality and

‘Throughout this paper, animals are reported as filtering if they cleared the water of suspended phytoplankton, even though at high algal densities most of the algal cells may have been rejected in pseudofaeces.

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adaptation rates influenced by tempera-ture.
Water was changed 3 times weekly, and at each change a heterogeneous mix-ture of phytoplankton was added (except in fresh water) so that observations on the filtering ability of the moilusks could be made. The algal mixture was predominantly Chlorella from a culture obtained by fertilizing sea water with commercial inorganic 5-10-5 fertilizer (Loosanoff & Engle, 1942). After mixing, salinity was checked by hydrometer and, if necessary, corrected to within 1% of the desired salinity.
Beach sand, collected from Cedar Island or the Machipongo River, was used as the substratum in all experiments except for those involving species incapable of burrowing. The depth of sand varied with the size of the experimental animals. Polyethylene, fiberglass or glass con-tainers were used in the experiments and for collecting and storing animals, sand and water.

SALINITY TOLERANCE BY SPECIES

Order Protobranchia
Family Solemyidae
Solemya velum Say (Tables 1,2,3)
The awning clam is found commonly in

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shallow muddy areas from Nova Scotia to Florida. It is relatively scarce in the collection area and is usually asso-ciated with Zostera marina at salinities above 15% (Wass, 1965).
Most Solemya survived direct transfer from either 30.8 or 34.4 %o to experimental salinities as low as 20% (Table 3). One clam out of a group of 30 survived transfer from 30.8% to 17.5%: none to lower salinities. However, clams survived at lower salinities after acclimation to intermediate salinities. A few survived at 12.5% after acclimation, but most of the Solemya were unable to survive below 15 %o .
Essentially the same salinity limits were established for burrowing and filtering as for survival. Again, the minimum salinities could be reduced to 12.5% by gradually acclimating clams to intermediate salinities. Frequently, filtering and burrowing were observed at salinities that eventually proved lethal.

Family Nuculidae

Nucula proxima Say

The nut clam is a common subtidal
mud dweller found from Nova Scotia to
Florida and Texas. Menzel (1964) lists
this species as occurring at salinities

TABLE 3. Response of Solemya velum Say to different salinities. Salinity at collection sites was 34.4 and 30.8%.

% Surviving Highest % burrowing Feeding (0= попе, R=
reduced, N=normal)
After After After
Salinity direct After direct After direct After
%o transfer acclimation transfer acclimation transfer acclimation

0 0 0 O O
29 0 0 O O
5.0 0 0 O O
ES 0 0 O O
10.0 0 0 0 O O
19:5 0 7.4 0 64.1 O R 15.0 0 84.6 0 100 O N 17.5 3.3 92 26.7 100 R N 20.0 86.3 92.3 100 100 М М 22.5 90.0 100 100 100 М М 25.0 89.7 100 100 100 М М
DD 90.0 100 N
30.0 96.7 100 N

SALINITY TOLERANCE OF MARINE BIVALVES 59

above 25% in Florida. It occurs in sand to silty sand, at salinities above 20% (Wass, 1965).

Family Nuculanidae

Yoldia limatula (Say)

The file yoldia is found along the East Coast from Maine to New Jersey but rarely in lower Chesapeake Bay (Wass, 1965). Natural distribution is probably limited to areas where salinity is above 20% (Wass, personal communica-tion).

Order Prionodontida

A major problem encountered with the Arcacea was their sluggish response to experimental conditions. In lower salinities they sometimes seemed narcotized and were often found gaping widely. They did not react to stimuli but, after being removed from the water, eventually closed. Some animals may have been removed as dead from earlier experiments before this trait was discovered. Even-tually, only putrescent individuals were considered dead.

Family Arcidae

Anadara transversa (Say) (Tables 1, 2, 4)
The little blood clam occurs commonly in subtidal mud from Cape Cod to Florida and Texas. It is common in Chesapeake Bay and its tributaries in intermediate salinities (15-25%) but is scarce at higher salinities (Andrews, 1953). It has been reported as occurring in areas where salinity varies from 3-42% (Parker, 1955) and 16-40% (Ladd, 1951). In Florida it is found at salinities above 25% (Menzel, 1964).
Anadara transversa were collected on 2 occasions from salinities of 17.5 and 25%, respectively. All died after direct transfer to salinities of 7.5%) and lower (Table 4). Only 2 clams out of 20 from 17.5% and none out of 20 from 25% survived direct transfer to 10%. Ninety percent of all clams survived direct transfer to salinities from 12.5- 30.0%. After acclimation, all clams sur-

vived at 10%, and 85% originally taken from 17.5% survived at 7.5%, although all those from 25% died at 7.5% (Table 4).
After acclimation, clams were trans-ferred directly to the opposite extreme of the salinity range. Transfers from 12.5 to 30% and 30 to 12.5% were effected without mortality. Only 2 out of 18 sur-vived transfer from 30 to 10%.
When clams were transferred directly to experimental salinities, suspended algae were cleared within the salinity range of 10-30%, but several days elapsed before normal filtration occurred below 17.5%o (Table 4). Filtering at 10 and 12.5% was always reduced unless clams were first acclimated at 15%. After acclimation, some clams cleared the suspended algae from the water irregularly at 7.5%o.
At no time did a majority of blood clams burrow into the substrate. Active clams usually climbed the sides of experimental containers by byssal attach-ment. Consequently, few burrowed after they became acclimated to experimental conditions (Table 4). At salinities close to the minimum for survival, burrowing was more obvious, presumably because clams were not active enough to reach the sides of the containers. Byssal attachment occurred at 7.5-30 %o but clams were slow to attach below 12.5% and then only after acclimation at intermediate salinities (Table 4).

Anadara ovalis (Bruguiere) (Tables 12.5)

The round blood clam is common and widely distributed from Cape Cod to the West Indies and the Gulf states. It is common subtidally in mud in both Chesapeake Bay and Eastern Shore lagoons. Andrews (1953) reported it as occurring in salinities above 15 %. Menzel (1964) found it at salinities above 25% in Florida.
All clams transferred directly from a ‘salinity of about 30% to 12.5% and lower died (Table 5). Only 45% survived direct transfer to 15% while 90-100% survived at all higher salinities. In 1 case

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a higher mortality occurred at 27.5% in
1 container. Clams in replicate containers
survived well.
Most blood clams survived at 15%
if salinity was reduced gradually. Nearly
85% of the blood clams acclimated at 17.5 and 20% survived when moved gradually to 12.5%. Clams surviving direct transfer to 15% were moved to 12.5%: all died. Although acclimated clams survived exposure to 10 and 12.5% for extended periods, it is doubtful they could survive indefinitely at these salinities.
Two groups of Anadara ovalis, ac-climated to intermediate salinities and then kept at 10% and 12.5% for 5 days, were transferred directly to 30%o. Only six out of 17 survived the transfer from 10 to 30% and none of these had burrowed when the experiment was con-cluded 13 days after the transfer. Of the 19 clams moved from 12.5 to 30%o, 18 survived but 11 days elapsed before the number burrowing was normal.
After direct transfer to experimental salinities clams were slow to start filtering but did clear the water of algae in salinities down to 20%o during the second day. Eventually, clams at 17.5%o filtered and cleared the water consistently. Although some filtering occurred at 10%, it was never normal when clams were transferred directly to salinities lower than 17.5%. Filtering occurred at 7.5%, after acclim-ation, but it was not consistent or normal below 15%.
Anadara ovalis were slow to burrow at all salinities and 5 days elapsed before 80% had burrowed, even at 30%. Seven days were required for a comparable percentage at 22.5-27.5% and even longer for those at 20%. At 17.5% and 15% a much lower percentage of clams burrowed. After acclimation, more clams burrowed at 17.5 and 15 % but burrowing activity was still reduced at these salinities. Acclimated clams also burrowed at 12.5%, but activity was irregular.
Comparatively few blood clams attached by byssus during the experi-ments. These clams were much less motile

than Anadara transversa and, unless they were near the sides of the container, had no substratum for attachment. Byssal attachment occurred at 17.5 %o and higher but was far less common below 22.5%o than at higher salinities. The minimum salinity for byssal attachment could be reduced to 12.5% by acclimating blood clams to intermediate salinities. However, only 1 clam attached by a byssus at 12.5 %o. A few attached at 15 and 17.5% but even after acclimation very few clams attached by byssus below 22.5%o.

Noetia ponderosa (Say) (Tables 1,2,6)

The large blood clam is common in shallow waters along the Atlantic Coast from Virginia to Key West. It is a common bivalve found on the seaside of the Eastern Shore in channels between Spartina marshes. It is also present in deep river channels and in high-salinity (above 20%) portions of Chesapeake Bay. Parker (1955) lists this species with a group found in an area where salinities ranged from 3-42%. Menzel (1964) records it in Florida in salinities above 25 %o. Some blood clams survived for a lengthy period after direct transfer to all salinities down to 12.5% (Table 6). However, mortality continued at 12.5% and 15%, and eventually all died except 1 clam at 15%. Mortality was heavy at 17.5%, but over 75% of the clams kept at 20-30%o survived. After acclimation to inter-mediate salinities, blood clams survived for long periods at 12.5 and 15% though fewer survived than at 17.5% and higher. Clams acclimated to 15, 17.5 and 20%0 in the Ist experiment were transferred directly to 30%. АП survived, and except for clams transferred from 15 to 30%, all were burrowing and feeding normally within 4 days. Only 3 out of 11 clams transferred from 15 to 30% burrowed. Blood clams filtered normally im-mediately after transfer to salinities of 25- 30%. Clams also filtered immediately after transfer to 20 and 22.5% o but did not consistently clear the water by filtering out the algae for almost 3 weeks. After the 3rd week, clams also filtered at 17.5 and 15%

SALINITY TOLERANCE OF MARINE BIVALVES 63

but never consistently cleared the water. Filtering was rarely observed at 12.5%o and was never normal. No filtering was observed below 12.5%. These limits were not extended by acclimation to in-termediate salinities.
Noetia ponderosa were especially sluggish about burrowing in the sand and required 3-4 days to dig in at 12.5-30.0%o salinity. At 27.5 and 30%, over 50% burrowed by the 10th day. Fewer clams burrowed after direct transfer to 22.5 and 20% but 50% dug in at 22.5% between the 10th and the 20th day. No clams burrowed at 20%o until the llth day, and only 17.8% burrowed at this salinity even after 70 days. The minimum salinity at which any clams burrowed was 17.5%o.
More clams burrowed at 20 and 17.5%o after being acclimated to intermediate salinities (Table 6). Even after acclimation, however, animals did not burrow at lower salinities.
Byssal attachment was usually observed in clams burrowed into the bottom. One clam was found attached to the poly-ethylene container by byssus at 17.5% and another at 20% after acclimation.

Byssal attachment was more common at 22.5% but still considerably less than at 25% and higher. Fewer clams attached by byssus during the 2nd experiment than during the Ist, probably because addi-tional sand left less substratum available for attachment. Byssal attachment was less common near the end of experiments.

Order Pteroconchida

Family Mytilidae

Mytilus edulis Linne

Along the eastern coast of North America, the edible mussel is found from the Arctic Ocean to South Carolina. In the collection area, permanent pop-ulations of M. edulis are apparently limited by temperature (Hutchins, 1947; Wells & Gray, 1960; Read, 1967) to the cooler, highly saline areas around the mouth of Chesapeake Bay, and to inlets between the barrier islands along the Eastern Shore. Catastrophic summer mor-
talities destroy new colonies periodically
established in warmer areas.
Andrews (1956) records M. edulis at
salinities above 15-18% in Virginia.
Dodgson (1928) reports survival from

TABLE 6. Response of Noetia ponderosa (Say) to different salinities. Salinity at collection sites was 30.6 and 32%.

% Surviving Average highest Feeding(0=none, R=
% burrowing reduced, N=normal)

Salinity After After After After After After
oo direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0
29 0 0 O
5.0 0 0 O
1) 0 0 O
10.0 0 0 0 0 O O IIS 0 19.8 0 0 O O
15.0 275 67.8 0 0 O R
Wee 22:5 91.2 3.1 18.2 O R
20.0 80.0 97.0 17.8 26.2 O N
22.5 1285 100 BET 41.0 R N
2510 85.0 97.4 65.5 52.6 N N
DD 95.0 82.1 N
30.0 92.5 84.2 N

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8.75-31%o, but notes defective byssus
formation below 16% and irregular
pumping below 12%. Schlieper (1953)
found a reduction of oxygen consumption,
ciliary activity and heart rate below 15%.
Prosser & Brown (1961), referring to other works of Schlieper, report M. edulis as occurring at 4-6%. Motwani (1955) gives the optimum salinity as 20-40% but says this is influenced by other environmental factors.
Bayne (1965) found that larval M. edulis failed to grow below 14% and that ор-timum salinity for growth was 18-26%. Apparently, М. edulis can survive at salinities less than 10%o, but about 15%o is necessary for optimum physiological func-tioning and reproduction.

Modiolus demissus Dillwyn

The ribbed mussel is widely distributed along the east coast from the Gulf of St. Lawrence to Florida (Menzel, 1964). It is found primarily in the intertidal zone where it occurs at a higher level than other bivalves. It is plentiful in seaside salt marshes with near oceanic salinities and is also found in estuaries where salinities are considerably below 20%. Andrews (1953) reports it at all salinities above 8-10 %o.
Wells (1961) experimentally determined a ‘salinity death point for M. demissus between 4 and 6%. Vernberg, Schlieper & Schneider (1963) reported a minimum salinity of 2% for ciliary activity of gill filaments and noted a sharp decrease in activity below 4%. In spite of the ability of this species to survive at low salinities, Nagabhushanam (1961) found a marked reduction in rate of pumping as salinities decreased from 32 to 10%. However, his results may show the effects of change in salinity rather than the effects of salinity per se.

Brachidontes recurvus Rafinesque

The hooked mussel has been reported as occurring from Cape Cod to the West Indies but is probably not commonly found living north of New Jersey. This mussel is common in subtidal areas of

Chesapeake Bay and its tributaries where salinities seldom exceed 20-25%. Pearse & Wharton (1938) found it at 5%, while Parker (1959) records it as belonging in an ‘assemblage’ that occurs from 3-40% . In the laboratory Chanley (1958) found that B. recurvus were not only alive but had “recognizable” gametes after 50 days exposure to salinities from 2.5-27%. Those kept in fresh water all died within 30 days. Allen (1960), however, reported 95% mortality of all mussels kept at salinities below 4.5% and heavy mortality below 6% in only 19 days. Nagabhushanam (1965) noted a decrease in heart rate from 35-31 beats per min. with a drop in salinity from 18-7.2%. A further decrease to 16 beats per min. occurred between 7.2 and 3.6%. At 1.8% the heart beat was only 3 beats per min. Again, these figures may indicate the effect of salinity change rather than salinity per se.
The minimum salinity for survival of this species is probably between 2.5 and 6.0%o.

Amygdalum papyria Conrad (Tables 1,2,7)

The paper mussel is found from Maryland south to the Gulf of Mexico. It is found in areas of moderate salinity such as the lower York and Rappahannock rivers in Virginia. Although abundant in limited areas, it is not generally distributed and is probably the least known of the mussels. It is apparently euryhaline and has been reported аз occurring in areas where salinity may be as low as 10% (Wass, personal com-munication) or as high as 45°%o (Parker, 1960).
All mussels transferred directly from about 20%o to O and 2.5% died (Table 7). In the 1st experiment all mussels trans-ferred to 5%o also died. However, 55% survived this transfer in the 2nd experi-ment. Best survival was observed at salinities from 12.5-20%o. The mortality at higher salinities (22.5-30%0) was not as abrupt as that at 0, 2.5 and 5% and occurred only after mussels had apparently

SALINITY TOLERANCE OF MARINE BIVALVES 65

adapted to salinities by filtering normally, burrowing, attaching by byssus and by nest-building.
The salinity tolerance limits of Amygda-lum papyria could be extended only slightly by moving them gradually to lower salinities. In the lst experiment 10 mussels surviving at 5% for 31 days died within 4 days after transfer to 2.5%o. In the 2nd experiment, however, 17 out of 23 mussels survived and were main-tained at 2.5% for 5-15 days before being moved to fresh water or before termina-tion of the experiment. Mussels did not survive when moved from 2.5% to fresh water.
After direct transfer to experimental salinities, some mussels burrowed in all salinities from 2.5-30%o though the per cent burrowing was reduced below 12.5%o. After acclimation in intermediate salin-ities, burrowing was apparently normal whenever mussels survived. However, a smaller percentage of mussels burrowed late in the experiment regardless of salinity. Some burrowing occurred at salin-ities which eventually proved lethal. Three mussels burrowed even in fresh water but did not repeat the performance when dug

up 2 days later.
Filtering was apparently normal at 10% and higher, though in the 2nd experiment it was initially reduced at 10%o. Normal filtering was occasionally observed at 2.5 and 5% after prolonged exposure to these salinities.
Byssal attachment and nest-building were possible at any salinity in which animals survived. A. papyria differs from the more familiar Mytilus edulis in this respect, since the latter is capable of surviving in salinities at which byssus formation is defective (Dodgson, 1928).

Family Ostreidae

Crassostrea virginica Gmelin

The American oyster is common inter-tidally and subtidally from the Gulf of St. Lawrence south to the Gulf of Mexico. It is widely distributed in Virginia where salinities are higher than 6-10%o (Andrews, 1953).
The oyster has been the subject of
much research and no attempt is made
here to present a complete review of all
pertinent literature. Only a few references
are cited to establish the salinity tolerance
of this species. Baughman (1947) and,

TABLE 7. Response of Amygdalum papyria (Conrad) to different salinities. Salinity at collection sites was about 21%o.

% Surviving Average highest Feeding (0= попе, R=
% burrowing reduced, N=normal)

Salinity After After After After After After
%o direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 O 10)
29 0 JON 5.0 50.0 O R
5.0 27.5 60.5 27.9 53.0 R R
aS 55.0 86.0 65.0 45.6 В В
10.0 70.0 94.6 TOD) 52.8 N N
125 82.5 9741 97.5 76.0 N N
15.0 95.0 90.0 100 100 N N
7.5 75.0 100 М М
20.0 75.0 100 N N
22.9 40.0 100 N N
25.0 45.0 97.5 N N
27.9 45.0 95.0 N N
30.0 37.0 90.0 N N

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more recently, Galtsoff (1964) give refer-
ences describing the salinity tolerance of
oysters.
Salinity limits for survival. Oysters can
survive over a wide range of salinities.
Ingle & Dawson (1951) report commercial production in areas with an annual salinity variation from 0-42.5%. Butler (1952) found self-sustaining populations in areas where salinity ranged from 0.2-3.6%o for 5 consecutive months annually. However, field observations by many investigators set the minimum salinity for indefinite sur-vival at 4-5% (Ryder, 1885; Arnold, 1868; Belding, 1912; Loosanoff, 1932; and many others). Parker (1960) observed that oyster reef formation occurs only between salinities of 10 and 30%o even though oysters are found outside these limits. The optimum salinity range for survival has been described as 14.1-22.2%o (Moore, 1900). Galtsoff (1964) states, according to the Venice system of classification of saline waters adopted by the International Association of Limnology and the Inter-national Union of Biological Sciences in 1958, that the range of salinity favorable for C. virginica falls within 2 zones, the polyhaline (30-18%) and the mesohaline 18-5 oo).
Laboratory experiments show close agreement with these field observations. Vernberg et al. (1963) found a marked decrease of ciliary activity in excised gill tissue below 4%. This agrees well with Fingerman s (1959) earlier report that ciliary activity occurred between 5 and 35%. According to Loosanoff (1952), some oysters survived when kept con-stantly at 5% although there was а high mortality. Survival was normal at 7.5%o and higher. Chanley (1958) reports similar salinity limits for recently metamorphosed C. virginica.
Salinity limits for growth and feeding. In Canadian waters, oysters apparently do not “fatten” or increase proportionally in dry weight when salinity drops below 20 %0 (Medcof & Needler, 1941; Medcof, 1944). According to Nelson (1923), the minimum salinity at which growth and feeding occur is based on the salinity

at which the oyster is acclimated. Loosanoff (1952), however, maintains that oysters adapt rapidly to salinity change and resume pumping activities within a few hours. He noted that a salinity of 10% is the minimum for normal growth of adult oysters. He observed feeding at 5% but says no growth occurred below 7.5%. Chanley (1958) reported slight growth of recently metamorphosed oysters at 5%, with optimum growth between 12.5 and 25%. Salinity limits for reproduction. The minimum salinity for gametogenesis has been reported as 6% by Butler (1949), who noted delay of gametogenesis until salinity rose above this level. Loosanoff (1952) reported 7.5 % as the minimum for gametogenesis.
Davis (1958) observed egg cleavage from 7.5-35%o with good development from 10-22.5%. Much higher limits were given by Amemiya (1926) who records egg development from 18-40.1%, with an optimum range of 19.3-35.1%o. Larval development has been reported as occurring between 14 and 39% (Amemiya, 1926), with optimum devel-opment between 25 and 29%. Clark (1935) is in general agreement with these ranges. Nelson (1909), however, found larvae in plankton samples when salinity was as low as 11.5%. Furthermore, Davis (1958) reported larval growth at as low as 5%, with the optimum between 17.5 and 22.5%. Under certain lighting conditions, Haskin (1964) found that activity of oyster larvae increased with increasing salinity and that all larvae failed to swim when salinity was less than 4.8%o.
Davis (1958) gives a minimum salinity of 10% for metamorphosis of oyster larvae, but Prytherch (1934) watched larvae metamorphose at 5.6%. The highest salinity at which he observed metamorphosis was 32.2 %0.
Discussion. There are several explana-tions for the apparent contradictions between these reports. Davis (1958) demonstrated that the salinity range for optimum egg development is depen-dent on the salinity at which game-

SALINITY TOLERANCE OF MARINE BIVALVES 67

togenesis occurred. Furthermore, it is likely that the degree and rapidity of change from environmental to experi-mental salinity influenced survival and development more than the actual salin-ities in some experiments. Davis & Calabrese (1964) have shown that the influence of temperature on the salinity tolerance of oyster eggs and larvae is minimal, though temperature tolerances are reduced at low salinities. Oyster eggs and larvae are known to be extremely sensitive to dissolved substances (Davis & Chanley, 1956), and possibly an excess or lack of some particular constituent in experimental salinities may have deter-mined limits rather than the actual salin-ity used. The concept of physiologically different races (Stauber, 1950) may also explain some differences. Although races of oysters have never been defined in terms of salinity, the wide distribution of this species could conceivably permit development of races with different salinity tolerances.

Family Pectinidae

Argopecten irradians Lamarck

The bay scallop is found from Nova Scotia to northern Florida and along the Gulf Coast to Texas. In Virginia this species was abundant in Eastern Shore seaside bays until the disappearance of eel grass in the early 1930's (Wass, 1965). Currently, bay scallops are found only rarely in the Eastern Shore lagoons where salinity is usually about 30%. According to Belding (1910), scallops are found in New England in areas where salinity ranges from 14.1-36.3%. In North Carolina, Gutsell (1930) reported a “distri-butional minimum salinity of 20% but noted that scallops survived exposure to 16.2% after unusually heavy rains. In Florida this species is found in salinities above 25% (Menzel, 1964). In the laboratory, Vernberg et al. (1963) noted a reduction in gill ciliary activity below 18% and a complete cessation of activity below 12%. They further observed that cold-acclimated scallops were more resistant to adverse

salinity than were warm-acclimated scallops.
The minimum salinity at which bay scallops survive would appear to be about 14 %o.

Anomia
1.2.8)

simplex Orbigny (Tables

The jingle is a common fouling organism found attached to shells, buoys, wharfs and other solid substrata from Cape Cod to Florida and in the Gulf of Mexico. It is found subtidally and is frequently associated with oysters. In Texas it has been reported from areas where salinity ranged from 11-40% (Ladd, 1951). It is found at salinities above 15% in Virginia (Andrews, 1953). Scheltema & Truitt (1954) found recently metamor-phosed individuals on test panels in Chesapeake Bay at salinities from 15.2- 26.3 %o.
Most Anomia simplex survived direct transfer from 31%o to salinities as low as 17.5% but direct transfers to salinities of 15% and lower resulted in complete mortality (Table 8). When salinities were reduced gradually, jingles survived to 12.5 and 10%, though it is doubtful that indefinite survival would have been possible at 10%. All jingles died in 5 days when kept at a salinity of 7.5%o even after acclimation. Half of the acclimated jingles survived a transfer directly from 12.5 to 30%o in 1 experiment, but in a 2nd experiment none survived this treatment. Animals transferred to 30% from salinities of 15% and above suffered по mortality and rapidly readapted to 30%o.
Anomia simplex filtered and reacted normally immediately after direct transfer to 22.5% and higher. Two ог 3 days elapsed before both filtering and the closing reaction were normal at 17.5- 22.5%. After acclimation, the minimum salinity at which these activities were nor-mal was 12.5%, though some filtering was observed as low as 7.5%.

Order Heterodontida

Family Carditidae

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Venericardia tridentata Say

Venericardia tridentata has been
reported as common in more shallow water
from North Carolina to southern Florida.
In Florida this species occurs in salinities
above 25% (Menzel, 1964). It is found only rarely in Virginia.

Family Corbiculidae

Polymesoda caroliniana Bosc

Polymesoda caroliniana is common in low-salinity muddy areas from Virginia south. Van der Schalie (1933) found this species where salinity ranged from fresh water (at low tide) to about 19%. He also observed that most clams survived for 2 weeks even when kept at oceanic salinities in the laboratory. Parker (1959) found P. caroliniana where salinity is always less than 10% but never in absolutely fresh water. In Virginia this species has been found only in the James River at salinities from almost fresh water to 15% (Andrews € Cook, 1951).

Family Dreissenidae

Congeria leucophaeta (Conrad)
(Tables 1,2,9)

This species is common in brackish

and fresh water from New York to Florida. In Virginia it is found at salinities below 10%o.
Congeria leucophaeta were collected at a salinity of about 7%. However, they were maintained in the laboratory at about 17.5%o for several weeks prior to these experiments. Most survived direct transfer to all experimental salinities from 0-30%o (Table 9). Byssal attachment and filtering were normal at these salinities. However, nearly 2 weeks elapsed before animals adapted to 0, 27.5 and 30%o. After this 2-week period, 65.3% of those kept in fresh water survived direct transfer to 30%o and adapted to that salinity. Only 11% (2 out of 18 clams) survived the reciprocal direct transfer from 30%o to fresh water, but these 2 clams did eventually show evidence of filtering and attach by byssus in fresh water. No mortality was associated with similar reciprocal transfers between 2.5%o and 27.5%. Within 1 week of this transfer, clams were attached and filtering
normally,

Family Lucinidae
Lucina multilineata Tuomey &
Holmes (Tables 1,2,10)
Lucina multilineata occurs commonly

TABLE 8. Response of Anomia simplex (Orbigny) to different salinities. Salinity at collection site was about 31%o.

% Surviving Feeding (0= попе, R=
reduced, N=normal)

Salinity After After After After
%o direct acclimation direct acclimation
transfer transfer

0 0 0
2,5 0 0
5.0 0 0
1.9 0 0 0 В
10.0 0 68.9 0 В 1925 0 86.6 0 М 15.0 0 97.3 0 М 17.5 76.7 98.1 М М 20.0 100 96.2 М М 22.5 83.3 94.7 М М 25.0 100 96.4 М М
21.5 94.3 N
30.0 96.3 N

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TABLE 9. Response of Congeria leucophaeta (Conrad) to different salinities. Salinity at collection site about 7 %o.

% Surviving Highest % Feeding (0=noné, R=
attaching reduce, N=normal)
by byssus

Salinity After After After
%o direct transfer direct transfer direct transfer

0 85.0 94.1 М
Po) 95.0 100 N
5.0 100 100 N
1) 100 100 N
10.0 100 100 N
1949 100 95.0 N 15.0 95.0 84.2 N 1785 90.0 94.4 N
20.0 95.0 100 N
22.5 90.0 94.4 М
25.0 100 95.0 М
DO 80.0 94.1 N
30.0 95.0 100 N

TABLE 10. Response of Lucina multilineata to different salinities. Salinity at collection site about
22 Vo.

% Surviving Average highest Feeding (0=none, R=
% burrowing reduced, N=normal)

Salinity After After After After After After
% direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 O
25 0 0 O
5.0 0 0 0 0 (0 O
1:9 20.0 100 10.0 95.0 R N
10.0 100 94.7 90.0 88.9 N N
12:5 100 100 80.0 100 N N
15.0 100 100 N
17.5
20.0
22.5 90.0 100
25.0
27.5 90.0 100 N
30.0 70.0 100 100 100 R N

from the shore to depths of over 700 ft mon in Virginia and is found in Chesa-from North Carolina to both coasts of peake Bay at about 20% (Wass, 1965). Florida. In Florida it is found in salinities Some Lucina multilineata survived above 25% (Menzel, 1964). It is less com- direct transfer from 22% to experimental

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salinities from 7.5-30% (Table 10).
Mortality was heavy after direct transfer
to 7.5% but negligible at higher
salinities. After acclimation to inter-
mediate salinities, survival was normal at
7.5%. Clams did not survive at 5% even though gradually acclimated to that salinity.
Burrowing and filtering were generally normal at all salinities in which clams survived.

Family Cardiidae

Laevicardium mortoni (Conrad) (Tables 1,2,11,12)

Morton s cockle is a small, active clam common in shallow, protected sandy areas from Cape Cod to Florida and the Gulf of Mexico. Ladd (1951) found this species in an area where salinity varies from 16- 42%o and Parker (1960) found it in an “assemblage” occurring in а salinity range of 30-45%. In Virginia, L. mortoni is fairly common from 15-25% and is periodically abundant in scattered areas of Chesapeake Bay and its tributaries. Laevicardium топот either quickly adapted to experimental salinities or died. Although some survived direct transfer from about 20% to salinities from 7.5-30°%0, there was appreciable mortality at 7.5 and 10% (Table 11).
The salinity limits could not be extended by acclimating clams in inter-mediate salinities, although the percent survival at 7.5, 10 and 30% was improved. There were minor differences between experiments. In the Ist experiment all of the 33 clams moved to 7.5 % were dead within 2 days. In the 2nd experiment clams survived and reacted normally at 7.5%. Almost no mortality occurred at 10% and higher in either experiment and по clams survived at 5%o.
At the conclusion of these experiments, clams surviving at low salinities were transferred directly to high salinities and survivors at high salinities were transferred directly to low salinities. Those transferred from 10 and 12.5% to 30% all died within 24 hours (Table 12). Only one clam out of

19 survived transfer from 10 to 27.5 %o. Surprisingly, all clams survived reciprocal transfers from 30% to 10 or 12.5%o. No mortality was associated with changes from salinities above 15% to 30%. Fewer clams burrowed after direct transfer to 7.5 and 10% than to higher salinities, and none burrowed at lower salinities. After acclimation to intermediate _ salinities, burrowing was normal at 10%o and im-proved at 7.5%. Some burrowing occurred at 5% after acclimation though clams eventually died at this salinity.
Filtering rapidly became normal at 10% and higher. Acclimated clams eventually filtered normally after exposure to 7.5% and some filtering occurred at 5.0%o.

Family Veneridae

Mercenaria mercenaria (L.)

The commercially important hard clam or quahog is abundant at moderately high salinities along the east coast from the Gulf of St. Lawrence to Florida. In Virginia this species is found in a variety of substrata intertidally and sub-tidally at salinities above 10% (Wass, 1965). Belding (1931) gives the salinity range of the quahog as 12.8-35%o, but says their survival is possible in salinities up to 46%. He does not believe that salinity influences growth within the normal range. Pratt & Campbell (1956) found hard clams occurring naturally from 21.4-31.9% and also expressed the opinion that growth was unaffected by salinity within this range. Turner (1953), however, reported no growth of adult clams at 19-21%o and optimum growth between 24 and 28%. Chanley (1958) reported similar levels for optimum growth of juveniles and growth decreasing with salinity to little or none below 17.5%. Minimum salinity for survival is given as 12.5%o. Larvae appear to require a slightly higher salinity than juveniles or adults. Metamorphosis did not occur below 20%o (Turner € George, 1955). Davis (1958) found larval growth improved with

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TABLE 11. Response of Laevicardium mortoni (Conrad) to different salinities. Salinity at collec-tion sites about 21%o.

% Surviving Average highest Feeding (0=none, R=
% burrowing reduced, N=normal)

Salinity After After After After After After
%o direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0
2.5 0 0 O
5.0 0 0 38.4 R
7.5 20.0 50.0 20.2 62.5 R R
10.0 85.0 98.7 83.5 99.1 N N
12.5 97.5 100 100 100 М М
15.0 97.5 100 100 100 М М
17.5 97.5 100 100 100 М М
20.0 92.5 100 100 100 М М
2230 95.0 100 100 100 N N
25.0 100 97.4 100 100 N N
27.5 97.5 100 100 100 N N
30.0 90.0 97.4 100 100 N N

TABLE 12. Survival of Laevicardium mortoni after direct transfer between the extreme experimen-tal salinities to which they had become acclimated.

Transferred to
(Salinity in %)

Transferred from
(Salinity in %o)

Le 30.0
10.0 30.0
10.0 27.5
12.5 30.0
15.0 30.0
17.5 30.0
27.5 17.5
30.0 15.0
30.0 12.5
30.0 10.0

increasing salinity from 15-27.5% and reports no metamorphosis below 17.5%o. He also reports that eggs developed normally from 20-35% with an optimum salinity about 27.5 %o.

Dosinia discus Reeve

This species is found along the east coast from Virginia to Florida but occurs only rarely in Virginia. Menzel (1964)

Number transferred Number surviving

20 0
19 0
19 1
19 0
17 15
18 18
20 19
20 20
18 18
14 13

lists it at salinities above 25% in Florida. D. discus is common in areas of North Carolina where the annual salinity range is from 6-38% but seldom less than 15% (Norton, 1947). In laboratory experiments D. discus survived 12 days in 50% seawater and 15-17 days in 75% seawater (Norton, 1947). Unfortunately, even controls were dead on the 19th day.

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Gemma gemma Totten
(Tables 1,2,13)

This small clam is very common along
the east coast from Labrador to North
Carolina (Sellmer, 1967). In Virginia it
is frequently found in abundance in sand where salinity ranges from 5-30%o (Wass, 1965).
Gemma gemma responded similarly in both experiments, adapted well to labora-tory conditions, and survived for pro-longed periods even at salinities that eventually proved lethal.
Clams survived direct transfer to salinities ranging from 10-30%. When transferred to 7.5%, all survived for several days, but then a slow steady mortality occurred and finally only 22.5% were still alive (Table 13). Salinities lower than 7.5% eventually proved lethal to all clams, although 1 clam did survive 51 days at 5%o.
After acclimation to intermediate salinities, survival of Gemma at 7.5°%0 was. normal. However, clams transferred to 5.0 °0 suffered a heavy mortality even after acclimation at 7.5%. All those transferred to 2.5% or fresh water died. When clams were moved from 7.5 to 25%o or from

30 to 10%, none died and filtering and burrowing were normal.
Clams were capable of burrowing after direct transfer to all salinities of 5% and higher. However, at least 3 weeks were required for normal numbers to burrow at 10%o and only a few burrowed at 7.5 and 5%o unless first acclimated at intermediate salinities. Burrowing was never observed at 2.5%o or in fresh water. Gemma filtered algae from the water at all salinities from 2.5-30°%o. However, filtering was not normal for 5-10 days at 10%o and was reduced and irregular at 7.5% and lower. Normal filtering occurred at 7.5% if animals were first acclimated at intermediate salinities, but was never normal at lower salinities. When the survivors were discarded at the conclusion of these experiments, juvenile Gemma were found in many con-tainers. Consequently, to determine reproductive ability at varying salinities, another experiment was started 23 April 1965, in which 10 Gemma were placed
in salinities ranging from 0-30%o. Оп 20
May, only clams at salinities from 10-30%o
were still alive. Juvenile clams were found
at all these salinities, indicating the ability
to reproduce from at least 10-30%.

TABLE 13. Response of Gemma gemma (Totten) to different salinities. Salinity at collection sites 23.2 and 20.0%.

% Surviving

Salinity After After After
%o direct acclimation direct
transfer transfer

0 0 0 0
9,5 0 0 0
5.0 0 63.9 10.0
10 22/9 100 52.9
10.0 100 98.5 100 125 97.5 99.0 100 15.0 100 100 100
17.5 97.5 100 100
20.0 100 100
22.9 100 100
25.0 100 100 100
РТО 97.5 100 100

Average highest
% burrowing

Feeding (0= попе, R=
reduced, N=normal)

After After After acclimation direct acclimation transfer

0 O
0 O R
53.8 O R
98.7 R N
99.4 N N
100 N N
100 N N
100 N N

100 N N
100 N N
100 N N

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Family Petricolidae

Petricola pholadiformis |L amarck (Tables 1,2,14)

This species is common in peat and clay from the Gulf of St. Lawrence to the Gulf of Mexico. Andrews (1956) found it at salinities from 15-25 % and Wass (1965) reported it from 20-30%. We have also collected it in areas where © salinity exceeds 30 %o.
Although all Petricola pholadiformis used in the 3 experiments were collected from the same locality, the salinity toler-ance varied considerably. The combined results of all 3 experiments are sum-marized in Table 14.
When clams were transferred directly from a salinity of 30-34 %o to experimental salinities, the minimum salinities at which they survived in the 3 experiments were 10, 12.5 and 17.5%, respectively, but mortality was heavy at 10%. The greatest tolerance range was noted in the experi-ment conducted at the coolest tempera-tures.

After acclimation at intermediate salinities, clams could tolerate a lower minimum salinity. However, even after acclimation the minimum salinity at which clams survived was different in each experiment (7.9. 10.0% sand # 1275250: respectively). After acclimation at minimum salinities, clams were trans-ferred directly to 30% with virtually no mortality. Within 1 or 2 days they had readapted to 30% and were burrowing and filtering normally. Apparently, slight-ly greater salinity changes could be tolerated when the change was toward 30 %o rather than away from it.
At minimum salinities for survival, comparatively few Petricola burrowed. At higher salinities virtually all surviving animals burrowed into the sand sub-stratum. After acclimation at intermediate salinities, a few clams burrowed at 5%,
but this salinity was eventually lethal.
Filtering was normal whenever sur-
vival and burrowing were normal. Even
after acclimation, feeding was reduced
at 10%o and lower.

TABLE 14. Response of Petricola pholadiformis (Lamarck) to different salinities. Salinity at collec-tion site 30-34%.

% Surviving Average highest Feeding (0= попе, R=
% burrowing reduced, N=normal)

Salinity After After After After After After
%o direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 O
25) 0 0 O
5.0 0 0 0 5.9 O O
eo 0 67.1 0 51.0 O R
10.0 15) 90.8 10.0 81.8 В В
12.5 67.5 96.2 75.0 95.2 N° N
15.0 75.0 98.5 Го 96.4 № М ee 95.0 97.0 100 98.4 N N
20.0 97.5 97.1 100 100 N N
29.5 90.0 100 100 100 М М
25.0 85.0 93.6 100 95.0 М М
271.9 92.5 100 N
30.0 82.5 100 N

°Except in 1 experiment where these salinities proved lethal.

Тейта agilis Stimpson (Tables 1,2,-
15)
Tellina agilis is found from the Gulf of St. Lawrence to North Carolina. It is com-mon in several areas in Virginia where the salinity is above 18% (Wass, 1965). Tellina were collected from an inter-mediate (20-24%) and а high (33%) salinity area. Two experiments were con-ducted with both groups. The results of all experiments are summarized in Table 15.
Most Tellina Нот 33% died when transferred directly to salinities below 20%, although a few survived at 17.5%. Most clams from 20-24% survived direct transfer to salinities from 12.5-30%о with a few surviving at 10%. After acclimation at intermediate salinities, both groups had similar minimum limits for survival. A few clams survived at 7.5%o but mortality was greater at salinities below 12.5%othan at higher salinities. Almost all clams burrowed rapidly at all salinities at which they survived. The apparent reduction in percent burrowing (Table 15) after direct transfer to 12.5- 17.5% reflects the failure of high-salinity

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Tellina agilis to burrow at salinities that were eventually lethal.
Filtering was normal at about 12.5% and higher. This limit was not appreciably lowered even when clams were acclimated to intermediate salinities.

Macoma balthica (L.) (Tables 1,2,16,
17)

This widely distributed species is com-mon along the eastern coast of North America from the Arctic Sea to Georgia. It is apparently euryhaline and is found in oligohaline as well as oceanic salinities. This species is abundant in soft substrates at low salinities (5-15%0) in Chesapeake Bay and its tributaries (Wass, 1965).

Macoma balthica survived direct trans-fer from 13-17% to salinities from 2.5- 30%o (Table 16) except in 1 experiment when the minimum salinity for survival was 5.0%. After acclimation at inter-
mediate salinities, virtually all clams
survived at 2.5-30%o and did not die
until 8-9 days in fresh water. Clams
that survived 5-6 days in fresh water
before being returned to higher salinities,

TABLE 15. Response of Tellina agilis (Stimpson) to different salinities. Salinity at collection sites 20, 24 and 33%o.

% Surviving Average highest
% burrowing

Feeding (O=none, R=
reduced, N=normal)

Salinity After After After After After After
%o direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 10)
25 0 0 O
5.0 0 0 0 0 O О
Lo 0 10.7 0 76.6 O R
10.0 15.0 66.2 25.0 97.4 R° R
1235 32.5 86.2 50.0 97.9 Re N
15:0 40.0 96.9 50.0 100 N° N
17.0 57.5 95.4 19.0 98.9 N° N
20.0 92.5 100 97.5 100 N N
220 92.5 100 100 100 М М
25.0 95.0 100 100 93.8 М М
97.5 92.5 100 М
30.0 82.5 100 М

“Except for the high salinity groups that died at this salinity.

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TABLE 16. Response of Macoma Баса (L.) to different salinities. Salinity at collection sites 13, 15.8 and 16.7%.

% Surviving Average highest
% burrowing

Salinity After After After After
%.o direct acclimation direct acclimation
transfer transfer

0 0 34.9° 0 100
265 60.0 97.0 66.7 100
5.0 96.7 100 100 100
leo 96.7 94.9 96.3 100
10.0 86.7 100 100 100 12.5 96.7 100 100 100 15.0 76.7 96.7
17.9 96.7 100
20.0 86.7 100 100 100
2975 80.0 100 96.7 100
25.0 96.7 100 100 100
27.5 96.7 97.4 100 100
30.0 83.7 95.8 100 100

“These survivors were all from 1 experiment and were exposed to fresh water only 5-6 days. Longer exposure would probably have been fatal.

TABLE 17: Survival of Macoma balthica after direct transfer between extreme experimental salinities at which they survived.

Transferred from Transferred to Number Number
(Salinity in %o) (Salinity in %o) transferred surviving

2.5 30.0 10 0
2.5 279 9 4
5.0 30.0 8 0
5.0 25.0 10 9
7.5 30.0 10 0
10.0 30.0 9 9 10.0 20.0 7 7 20.0 10.0 6 6
22.5 7.9 5 5
25.0 5.0 9 8
27.5 2.5 9 8
30.0 7.5 10 10
30.0 5.0 10 10
30.0 2.9 9 9

would probably have died if they had quickly killed when transferred from remained in fresh water. salinities of 7.5% and lower to 30%. Clams were not harmed by sudden Reciprocal changes from 30% to 7.5, 5.0 transfer from 10 to 30%, but they were and 2.5% resulted in no mortality and

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clams adapted quickly to the new salinity
(Table 17).
Virtually all surviving clams burrowed.
Even in fresh water all clams burrowed
after acclimation at 2.5%. Within a few
days when clams were dug up, they failed to burrow again and died.
Масота balthica feeds primarily on detritus rather than suspended matter and accurate observations on its feeding or filtering were not possible.

Macoma mitchelli Dall (Tables 1,2, 19.19)
This species is abundant in many of the

brackish water creeks of Chesapeake Bay at salinities from 2-20%o (Wass, 1965). Some Macoma mitchelli survived direct transfer from field salinities (14.9- 17%) to all salinities from 2.5-30%o. Mortality at 2.5 and 5% was greater after such a transfer than at other salinities (Table 18). Surprisingly, clams taken from a salinity of 14.9%o were killed by transfer to 2.5% and only 4 out of 10 survived at
5%. Over 70% of the clams taken from
17%o survived when transferred to these
salinities. After acclimation at inter-
mediate salinities, no unusual mortality
occurred at 2.5-30%. When clams were

TABLE 18. Response of Macoma mitchelli (Dall) to different salinities. Salinity at collection sites 14.9 and 17.0%.

% Surviving Average highest
% burrowing

Salinity After After After After
%o direct acclimation direct acclimation
transfer transfer

0 0 0 5 1128
225 33:0 95.6 14.3 76.3
5.0 60.0 97.9 72.3 79.3
7.5 90.0 100 72.8 81.4
10.0 100 96.3 85.0 81.7 12.5 90.0 100 1225 88.9 15.0 95.0 90.0
LS 90.0 100
20.0 90.0 100 90.0 100
22.5 100 100 85.0 96.7
25.0 80.0 100 81.6 92.0
С, 95.0 94.5 85.0 94.3
30.0 80.0 90.0 95.0 91.1

TABLE 19. Survival of Macoma тисйей after direct transfer between extreme experimental salinities to which they had become acclimated.

Transferred to
(Salinity in %o)

Transferred from
(Salinity in %o)

Number transferred Number surviving

2.5 30.0
5.0 30.0
7.5 30.0
10.0 30.0
30.0 12.5
30.0 10.0
30.0 7.5
30.0 5.0
30.0 2.5

18 0
10 0
1. 0
9 1
6 5
10 10
17 14
10 3
18 0

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moved to fresh water, they eventually died though some survived for nearly 3 weeks. Rapid salinity increases of 20%o and more killed most clams (Table 19). Rapid salinity decreases of 25% resulted in little mortality and a few clams survived a rapid salinity decrease of 27.5 % . Macoma mitchelli burrowed at all experimental salinities including fresh water. However, a lower percentage of clams burrowed after direct transfer to O and 2.5%. After acclimation there was little difference in burrowing ability of clams from 0-30% although clams in fresh water eventually weakened and died. Macoma mitchelli did not clear the water of algae satisfactorily throughout the experiments. Possibly they are primarily detritus rather than filter feeders. Some filtering did occur at 2.5-30%o.

Macoma tenta Say

Macoma tenta is found from Cape Cod to Florida in a sandy substratum in shallow water. In Florida it occurs in sandy mud at salinities above 25% (Menzel, 1964). In Virginia it is found in silt-clay substrata at

—]A N

salinities from 20-30% (Wass, 1965).

Family Semelidae

Abra aequalis Say

Abra aequalis is abundant from North Carolina to Texas. It is found at salinities above 25%o in Florida (Menzel, 1964). In Virginia it is rarely encountered (Wass, 1965).

Family Donacidae

Donax variabilis Say (Tables 1,2,20)

Donax variabilis, the colorful toquina of southern beaches, is common from Virginia to Florida and Texas. Because of its unique habitat in the surf zone of sandy beaches, it is seldom found at salinities below 30%. In Virginia, D. variabilis is found on ocean beaches during the summer and autumn at salinities above
30%o.
Although the 2 experiments involving
this species were conducted under
different temperature regimes and with
clams of different sizes, the results were

TABLE 20. Response of Donax variabilis Say to different salinities. Salinity at collection sites 33- 35%.

% Surviving Average highest Feeding (0=none, r=
% burrowing reduced, N=normal

Salinity After After After After After After
%o direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 O
25 0 0 O
5.0 0 0 O
AD 0 0 0 71.9 O R
10.0 0 38.5° 0 94.8 O R
PA) 0 94.6 0 100 O N
15.0 0 100 120 99.3 O N
1725 20.0 99.2 100 100 R N
20.0 60.0 100 100 100 N N
DS 85.0 98.7 100 100 N N
25.0 92.5 100 100 100 N N
PAT) 97.5 100 N N
30.0 92.5 100 N N

“This salinity would probably have eventually killed all.

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remarkably similar.
Donax variabilis survived direct trans-
fer to salinities from 17.5-30%, but
heavy mortality was associated with trans-
fers below 22.5% and only 20% survived
direct transfer to 17.5% (Table 20). The relatively narrow salinity limits indicated in the first phase of these experiments were extended appreciably by acclimating coquinas to intermediate salinities. After acclimation, clams sur-vived well and reacted normally at salinities as low as 12.5 %o.
At the conclusion of the acclimation phase of the experiments, surviving Donax variabilis were transferred directly to 30%. Only 1 out of 36 clams died when transferred from 12.5% (the minimum salinity at which clams lived) to 30%. None died when transferred from 15 to 30%o.

Donax variabilis burrowed and filtered immediately at all salinities at which they survived. In fact, several dug in and fed at either 15%o after direct transfer, or 7.5 and 10%o after acclimation even though these salinities eventually proved lethal.

Family Sanguinolariidae

Tagelus plebeius Solander (Tables 12.41.22)

This species is listed as common from Cape Cod to Florida and in the Gulf of Mexico. It is 1 of the more common bivalves of Virginia. Andrews (1956) reports it as euryhaline and common above 10%o.
Tagelus plebeius were collected from intermediate salinity areas (about 20%o) for 3 experiments. These clams survived direct transfer to salinities from 2.5-30%o, though only about 1/3 survived at 2.5%. In the 4th experiment clams were obtained from nearly oceanic salinities. None of these clams survived direct transfer to either 2.5 or 5% and only 10% survived at 7.5%. Survival from 10-30% was normal. After acclimation at inter-mediate salinities, clams from both areas survived well at 2.5% and higher. None
survived when transferred to fresh water.
The combined results are shown in Table
21. After clams from the intermediate
salinity area were acclimated to a salinity
of 30%, they were transferred directly to

TABLE 21. Response of Tagelus plebeius Solander to different salinities. Salinity at collection sites 14.9, 20.4, 21.8 and 32.4%.

% Surviving

Salinity After After After
%o direct acclimation direct
transfer transfer

0 0 0 0
25 27:5 86.9 19.2 5.0 12.5 81.2 46.4
10 12:0 95.8 56.1 10.0 97.5 95.4 78.9 12.5 97.5 98.8 87.2 15.0 100 91.1 87.5 125 100 83.9 82.5 20.0 97.5 94.] 79.4 22.5 100 89.5 Wed
25.0 97.5 100 91.9
Fico 97.5 100 80.0
30.0 100 95.6 90.0

Average highest
% burrowing

Feeding (0= попе, R=
reduced, N=normal)

After After After
acclimation direct acclimation transfer

0 O O
81.1 O R
out R N
79.6 R N
85.9 N N
85.2 N N
85.7 N N
81.3 М М
87.6 М М
81.8 М М
78.9 М М
90.0 М М
86.0 М М

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TABLE 22. Survival of Tagelus plebeius after direct transfer between the extreme experimental salinities to which they had become acclimated.

Transferred to
(Salinity in %o)

Transferred from
(Salinity in %o)

2.5 30.0
2.5 27.5
2.5 25.0
5.0 30.0
7.5 30.0
10.0 30.0
12.5 30.0
15.0 30.0
30.0 7.5
30.0 5.0
30.0 2.5

salinities of 7.5 and 5.0% without appreciable mortality (Table 22). Almost 2/3 survived direct transfer to 2.5%, whereas clams from the high salinity area were killed by comparable _ salinity changes. When clams from both groups were acclimated to 2.5 and 5% and then transferred directly to 30%, all died. Transfer from 7.5 to 30%, 2.5 to 27.5%, and 2.5 to 25% also resulted in heavy mortality (Table 22).
Clams burrowed and filtered after direct transfer to salinities of 2.5-30%o. However, activity was reduced below 10%o (Table 21). After acclimation, burrowing and filtering were not appreciably increased at salinities from 2.5-30%o.

Tagelus divisus Spengler

This species also is found from Cape Cod to Florida and in the Gulf of Mexico. Fraser (1967) studied a Florida population living in an area where salinity ranged from 29.1-39.3% . In Virginia it has been found only subtidally in moderately high salinity water.

Family Solenidae

Ensis directus Conrad (Tables 1,2,23)

The common razor clam is found from Labrador to South Carolina and probably Florida. In Virginia, Wass (1965) lists it as an intertidal and subtidal form found

Number transferred Number surviving

20 0
20 4
9 5
34 0
24 11
15 12
15 14
Y 6
29 29
19 18
38 25

above 20%. In some areas of Chesapeake Bay it is common at much lower salinities (Pfitzenmeyer, personal communication). Under experimental conditions Chanley (1958) found that E. directus could be acclimated to survive at 7.5-28%. How-ever, a rapid salinity change of 15% within this range was lethal.
Ensis, from nearly oceanic salinities, sur-vived direct transfer to experimental salinities of 17.5 and 12.5% in the 2 experiments conducted with this species. However, mortality was heavy below 20

TABLE 23. Response of Ensis directus Conrad to different salinities. Salinity at
collection site 32%o.

% Surviving
Salinity After After
%o direct transfer acclimation

0 0
2.5 0 0
5.0 0 80.9
7.5 0 95.3
10.0 0 98.4
12:5 5.0 100
15.0 20.0 100
178 50.0 100
20.0 95.0 98.2
22:9 95.0 100
25.0 95.0 100
27.5 90.0
30.0 95.0

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and 17.5% for the 2 experiments (Table
23). Clams were acclimated to survive, at
least for brief periods, at salinities as low as
5%. All clams survived direct transfer
from 12.5 to 30% but transfers from 10%o
and lower to 30% were lethal.
All surviving clams burrowed normally at salinities of 5%o and higher. Some clams burrowed at 2.5% but eventually died. Filtering was slightly reduced below 10% but otherwise was normal wherever clams survived.

Solen viridis Say (Tables 1,2)

The green razor clam is fairly common in shallow water sand flats from Rhode Island to Florida and in the Gulf states. In Virginia it is found infrequently in sand bars of the barrier islands and therefore only in high-salinity water. Solen viridis are comparatively rare in Virginia and enough were found for only | experiment. Unfortunately, they survived poorly in the laboratory and the experiment had to be terminated after 8 days. At this time it seemed likely that direct transfers from 33-34% to experi-mental salinities of 17.5 to 20%o could be tolerated.

Clams were very active and some burrowed immediately after transfer to all salinities, including fresh water.

Family Mactridae

Spisula solidissima (Dillwyn) (Tables 1,2,24)

The surf clam, or skimmer, is abundant from Nova Scotia to Florida and from Florida to Texas. Under natural conditions it is not found below 28% but may be able to tolerate much lower salinities. Welch (unpublished manuscript) found the minimum lethal limit between 15 and 20%. He further stated that eggs of this species do not develop at 22% or lower, but larvae survive and grow at 16%. Schechter (1956) places the minimum tolerance of both eggs and sperm of Spisula solidissima at “40% sea water” or about 15%. Eggs in the “polar-body stage, however, disintegrated at this salinity.
Some surf clams survived direct transfer
to all salinities from 15-30% (Table 24).
Mortality was heavy at 15%, however,
and in the 2nd experiment clams failed
to survive when transferred to this salinity.

TABLE 24. Response of Spisula solidissima (Dillwyn) to different salinities. Salinity at collection sites 32-34 %o.

% Surviving Average highest
% burrowing

Feeding (0= попе, R=
reduced, N=normal)

Salinity After After After After After After
% direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 О
2.5 0 0 O
5.0 0 0 O
1.0 0 0 0 60.0 O O
10.0 0 80.3 0 100 О В
12:5 0 96.0 0 100 В М
15.0 25.0 98.4 100 100 К М
5 76.8 100 100 100 N N
20.0 68.9 98.9 100 100 N N
22.0 86.4 100 100 100 N N
25.0 95.0 100 100 100 N N
225 97.5 98.2 N N
30.0 75.0 100 N N

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Spisula solidissima failed to remain tightly closed at lethally low salinities and, con-sequently, died rapidly. After acclimation to intermediate salinities, the lower limits for survival were extended and 75% of the clams exposed to 10% survived. Over 90% of those exposed to 12.5% and higher survived. All clams transferred to 7.5% died. All surviving clams were transferred directly to 30%. Thirteen of the 16 moved from 10 to 30%o survived the change eventually readapted to that salini-ty. All clams transferred from 12.5%0 and higher survived and adapted to 30%0 within a few days.
Burrowing was normal at all salinities at which clams survived, though at lower salinities there was often a period of adjustment before normal burrowing occurred. Some clams burrowed at 7.5%o before they died.
Clams filtered in all containers in which they survived. Some limited filtering occurred at lethal salinities before clams died (12.5% after direct transfer and 7.5% o after acclimation).

Mulinia lateralis (Say) (Tables
1.2 95.96)

This small clam is a common to abundant inhabitant of sandy substrata in shallow water from Maine to Texas. Parker (1960) lists it as occurring where salinity ranges from 18-80%. Ladd (1951) found few М. lateralis between 4 and 9%o but many from 10-40%. Nagabhushanam (1964) found that visceral ganglia of this species lose their secretory granules at low salinities.
In Virginia, fluctuating populations of this species are common above 8% (Wass, 1965), but less common above 25%.
Two samples of Mulinia lateralis, collected from an area where the salinity was between 16 and 17%o, survived direct transfer to experimental salinities from 5-
30%. Although mortality was heavy in 1
group at 5%, virtually no mortality oc-
curred at higher salinities. When clams
were transferred from environmental
salinities of 20 and 24.6 %, the minimum

TABLE 25. Response of Mulinia lateralis Say to different salinities. Salinity at collection sites 16.5, 16.9, 24.0 and 24.6 “bo.

% Surviving Average highest
% burrowing

Feeding (0= попе, R=
reduced, N=normal)

Salinity After After After After After After
%o direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 5.0 20.0 O O
29 0 65.5 WED 75.3 O R
5.0 30.0 87.8 32.5 100 R N
то 60.0 92.0 66.1 100 В М
10.0 97.5 99.1 100 100 М М
119445) 100 98.9 100 100 N N 15.0 100 100 100 100 N N
170) 97.5 100 100 100 N N
20.0 100 100 100 100 N N
22.9 97.5 100 100 100 N N
25.0 100 100 100 100 N N
29 97.5 100 100 100 М М
30.0 100 100 100 100 М М

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TABLE 26. Survival of Mulinia lateralis after direct transfer between the extreme experimental salinities to which they had become acclimated.

Transferred from Transferred to Number transferred Number surviving (Salinity in% o) (Salinityi n %o)

2.5 30.0 20 0
5.0 30.0 2 0
7.5 30.0 18 9
10.0 30.0 10 6
12.5 30.0 10 1 30.0 12.5 10 10 30.0 10.0 18 18 30.0 7.5 40 37 30.0 5.0 19 7 30.0 2.5 20 0

salinities at which they survived were 7.5
and 10%, respectively.
After acclimation at intermediate
salinities, most clams survived at 5%.
Clams from low-salinity areas survived
at 2.5%, a salinity lethal to Mulinia lateralis from the 2 high-salinity areas even after acclimation at intermediate salinities (Table 25). No clams survived in fresh water. Clams © surviving at 2.5 and 5.0% were killed when trans-ferred directly to 30% (Table 26). Although all clams died in a reciprocal transfer from 30 to 2.5%0, over 1/3 sur-vived transfer from 30 to 5%. Fifty per-cent survived transfer from 7.5 to 30%o but over 90% survived the reciprocal transfer. Appreciable mortality occurred even when clams were transferred from 10 and 12.5%0 to 30%o, but no clams died when transfers were made from 30 to either 10 ог 12.5%o. Some clams burrowed after direct trans-fer to all salinities including fresh water. The number burrowing was not normal, however, at salinities that were eventually lethal. Clams filtered algae from the water at all salinities at which they survived.

Rangia cuneata (Gray) (Tables
1,227)

Rangia cuneata is a common species in fresh to brackish water along the coast from Maryland to Texas (Pfitzenmeyer & Drobeck, 1964). In Virginia it is common

in low-salinity areas of Back Bay and the James River (Wass, 1965). Parker (1960) found R. cuneata in fresh water and in areas where salinity did not exceed 10%. Ladd (1951) noted it as abundant where salinity ranged from 4-9% but scarce from 13-25%. Parker (1965) observed that Rangia were found in Texas only where the average annual salinity was less than 18%. Well-established populations were studied in Lake Pontchartrain where salinity varied from 1.5-9.8% annually (Fairbanks, 1963). Godwin (1967) reported finding Rangia in Georgia at salinities from 2.5-11.5%o, with commerical concen-trations at 3.5-4.5%o. Gunter (1961) noted that larger Rangia seemed to be found in areas where salinity was lower. Pfitzenmeyer & Drobeck (1964) observed the same phenomenon in Potomac River populations where they found Rangia at salinities from 5.7-11.8%o.
In the laboratory, Allen (1961) was able to keep Rangia alive at several salinities from fresh water to 25%. He noted that the concentrations of amino acids in-creased with salinity to 17% but decreased with further salinity increase.
Rangia cuneata were collected from salinities of about 5% and transferred directly to experimental salinities. In l experiment mortality was high after direct transfer to 22.5% and higher. In the second experiment only 1 clam sur-vived at salinities of 20% and higher and

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TABLE 27. Response of Rangia cuneata (Gray) to different salinities. Salinity at collection site about 5%o.

% Surviving

Salinity After After
%o direct acclimation
transfer

0 50.0 100
2.5 100
5.0 100
7.5 100
10.0 100 100
1225 100 100
15.0 97.5 100
1723 82.5 100
20.0 47.5 100
2975 15.0 100
25.0 29.5 100
275 2.5 100
30.0 0 100

Highest %
burrowing

After After
direct acclimation
transfer

100 100
100
100
100
100 100
100 100
100 100
100 100
100 100
100 100
100 100
100 100
0 100

several died even at 17.5%. All clams survived direct transfer to fresh water in the lst experiment while a similar transfer was fatal to all clams in the 2nd experi-ment. These results are summarized in Table 27.
After acclimation at intermediate salin-ities, Rangia cuneata survived at all experi-mental salinities including fresh water and 30%. At the conclusion of the experiments surviving clams were moved from 30% to 5%0 without mortality.
All Rangia cuneata dug in and filtered normally at all experimental salinities at which they survived.

Family Myacidae

Mya arenaria (L.)

The commerically important soft clam is found from Labrador to North Carolina. It is known to be a euryhaline form and has been found at salinities from 6.3-32.4% (Belding, 1930; Kellogg, 1901). Pfitzenmeyer & Drobeck (1963) found it at salinities as low as 3%. In Virginia, soft clams are abundant above 10% in Chesapeake Bay and its tributaries (Wass, 1965). They are also present but

scarce in seaside bays where salinity may reach 35%. In the laboratory, soft clams from several different geographical areas had different minimum salinities at which they survived but all could be acclimated to survive at 2.5%o (Chanley, 1958). Stickney (1964) found that about 1% of Mya eggs developed to normal straight hinge larvae at 8%o. Larvae grew fairly well at 10%o but optimum salinities were higher. Salinity requirements of eggs and larvae were determined by the environment of the adult.

Family Pholadidae
Barnea truncata (Say) (Tables 1,2,28)

This species occurs from Maine to Florida and is common from Massachu-setts south in clay, soft rock or wood (Turner, 1956). In Virginia it is commonly found in peat (Wass, 1965) from 16-35%. Some Barnea survived direct transfer from 30-34% to 12.5% and 15% but mortality was greater than after transfer to salinities above 15% (Table 28). All clams transferred to salinities of 10%o and lower died. After acclimation at inter-

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TABLE 28. Response of Barnea truncata (Say) to different salinities. Salinity at collection site 33-
35 %o .

% Surviving Feeding (0=none, R=
reduced, N=normal)
Salinits After After After After
%o direct acclimation direct acclimation
transfer transfer

0) 0) O
2.9 0 0 O R
0 0 42.1 O R
То 0 73.8 O R
10.0 () TDA he O R
[225 30.0 99.1 В М 15.0 67.5 100 R N 17.5 95.0 98.0 N N
20.0 90.0 94.5 N N
22:5 95.0 93.8 N N
29:0 92.5 97.4 N N
27.9 95.0 N
30.0 95.0 N

"When clams that survived the direct transfer to 12.5 were moved to 10%, all died. Almost all
0
clams acclimated at other salinities survived when moved to 10%.

mediate salinities, clams survived well at
salinities down to 10%. Some clams sur-
vived at 7.5 and 5.0% but the higher
mortalities at these salinities suggest that
they might eventually be lethal. Direct
transfers of clams from 5, 7.5, and 10% to 30% killed all clams. Thirteen out of 24 clams survived the transfer from 12.5 to 30%, and 14 out of 19 clams survived transfer from 15 to 30%.
Filtering was normal Нот 17.5-30%o after direct transfer. No filtering occurred at 10°%0 and lower and filtering was re-duced at 12.5 and 15%. After acclimation, filtering was only slightly reduced at 10%o and normal at higher salinities. Some filtering was observed at 2.5% but filtering was definitely reduced below 10%o.

Barnea truncata are incapable of making new burrows as adults; consequently, observations on the effect of salinity on burrowing were not possible.

Diplothyra smithii (Tryon)

This species is found boring into shell

and, rarely, wood from Massachusetts to Florida. It is common in the south but scarce from Virginia north. Menzel (1964) lists it as occurring at salinities above 25%o.

Martesia cuneiformis (Say)

Martesia cuneiformis can be found boring in wood from North Carolina southwards. It probably does not normally occur in Virginia (Turner, 1956). Menzel (1964) lists it at salinities above 25%o.

Cyrtopleura costata (L.) (Tables 15=2,, 29)

The angel wing is found in sand to soft, sticky mud from Massachusetts to Florida and Texas (Turner, 1956). Ladd (1951) reports it as occurring from 16-40 %. It is a common Virginia species in suitable substrata and is found where salinity is above 10% (Wass, 1965). Cyrtopleura costata survived direct transfer from about 20%o to salinities from 7.5-30% . After acclimation in inter-mediate salinities, clams survived at

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TABLE 29. Response of Cyrtopleura costata (L.) to different salinities. Animals were raised in the laboratory at a salinity about 20%.

% Surviving Feeding (0= попе, R=
reduced, N=normal)

Salinity After After After After
%o direct acclimation direct acclimation
transfer transfer

0 0 0 O
2.5 0 0 O R
5.0 0 100 О В
7.0 100 100 R N
10.0 100 100 R N 12.5 100 100 R N 15.0 100 100 N N 17.5 100 100 N N 20.0 100 100 N N
22:5 100 100 N N
25.0 100 100 N N
27.5 100 100 N N
30.0 100 100 N N

2.5% for lengthy periods but eventually salinities.
died and 5% was the minimum salinity Culliney (personal communication) in which clams survived.
After direct transfer from 20%, the rate
of filtering was reduced at 12.5% and
lower. No clams filtered below 7.5%.
When animals were acclimated in inter-
mediate salinities, feeding was normal from 7.5-30% but reduced or absent at lower salinities.
Cyrtopleura costata were incapable of digging new burrows, so no observations on the influence of salinity in burrowing were possible.

Family Teredinidae

Bankia gouldi (Bartsch)

This is a common east coast shipworm found from New Jersey to Florida. This species in plentiful in Chesapeake Bay but is scarce or absent in high-salinity oceanic water. Clark (1954) reports its minimum salinity as 10%. This agrees closely with the observations of Scheltema & Truitt (1954) who found that larval B. gouldi set on test panels at salinities from 9-30%. Within this range, fewer shipworms were found at lower

reports that Bankia gouldi larvae survive but are “barely growing” in a constant salinity of 10%o.

Teredo navalis L.

Teredo navalis has a world wide dis-tribution and is considered euryhaline. It is the common shipworm at oceanic salinities but rare in Chesapeake Bay.
The salinity tolerance of this species is fairly constant throughout its range and the minimum salinity for survival has been listed as 5, 6, 7, and 8% (Blum, 1922; Miller, 1926; Clark, 1954; Kudinova-Pasternak, 1960; Soldatova, 1961). These observations were made over a geographic range from San Francisco to the Black Sea and over a period of nearly 40 years, yet they differ by only 3%. These same authors report an optimum salinity of 12- 25 or 28% for survival of T. navalis. Blum (1928) found that activity of T. navalis was reduced when salinity was below 7.5% but that they could survive at 4%o for a month. However, shipworms eventually died when kept at 4%. M'Conigle (1927) found activity reduced

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at 13% and entirely stopped at 10%.
Both he and Soldatova (1961) reported
that 40%o is the upper lethal salinity.
The minimum salinity for larval devel-
opment has been reported as 9%
(Miller, 1926) and 12% (Kudinova-Pasternak, 1962). M Conigle (1927) found some development at 7.5% but lists this as an “unfavorable” salinity. Culliney (personal communication) reports that larval T. navalis were reared to the pediveliger stage at a constant salinity of 7.5%. Growth, however, was very
slow.

Family Lyonsiidae

Lyonsia hyalina (Conrad) (Tables 1,2,30)

Lyonsia hyalina Conrad is common in shallow water in sandy substrata from Nova Scotia to Florida. In Virginia it is found at salinities above 15% (Wass, 1965) and in Florida above 25 % (Menzel, 1964).
Lyonsia hyalina were available for only l experiment. When transferred directly from 20% to experimental salinities, survival was good at salinities from

12.5-30% (Table 30). Four out of 10 sur-vived at 10%. Salinities lower than 10% were lethal. Clams could be acclimated to 7.5% but all died when transferred to 5.0%. Clams began dying from unknown causes before further transfers could be made and the experiment was discon-tinued.
Lyonsia hyalina burrowed actively at all salinities at which they survived. A limited amount of filtering was observed at 5%o though these clams eventually died. Filtering was also reduced at 10% after direct transfer and at 7.5% after acclima-tion to intermediate salinities. Clams filtered normally at all other salinities.

DISCUSSION

During the course of these experiments it became apparent that the minimum salinity tolerated by a species was variable. Acclimation at intermediate salinities usually extended tolerance limits.
However, after acclimation, the minimum
salinity in which a species survived
sometimes varied from 2.5-5% between
replicate experiments. Some species
collected from the same location at com-

TABLE 30. Response of Lyonsia hyalina Conrad to different salinities. Salinity at collection site 20%00.

% Surviving Average highest Feeding (0=none, R=
% burrowing reduced, N=normal)

Salinity After After After After After After
%60 direct acclimation direct acclimation direct acclimation
transfer transfer transfer

0 0 0 O
20 0 0 O
5.0 0 0 0 0 O R
139 0 100 0 100 O R
10.0 40.0 100 100 100 R N
12:5 90.0 100 100 100 N N
15.0 90.0 100 100 100 N N
17:5 100 100 N
20.0 100 100 N
22.5 100 100 N
25.0 90.0 90.0 100 100 N N
DO 100 89.9 100 100 N N
30.0 80.0 100 100 100 N N

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parable temperatures and salinities but in different months had different minimum tolerance limits, indicating a seasonal variability in salinity tolerance. This difference was not related to reproductive condition or to the appearance of the animals tissues.
Occasionally, minor differences could be attributed to the different temperatures at which experiments were conducted. However, in most cases, the temperature primarily affected the rate of response to experimental salinities rather than changing the tolerance limits. For example, burrowing, filtering or mortality usually occurred more rapidly at higher temperatures, but the salinities at which these occurred were about the same regardless of temperature.
In some cases, salinity at the time of collection appeared to influence the range of salinity to which bivalves could adapt. Animals collected when salinity was low sometimes had higher tolerances at minimum salinities than those of the same species collected from high salinity waters. This difference persisted even after laboratory acclimation at intermediate salinities. Perhaps longer and more gradual acclimation in the laboratory would have eventually eliminated this difference.
Some species such as Solemya velum, Solen viridis and Tagelus plebeius were not adaptable to laboratory conditions and their vital activities were reduced or mortalities increased as experiments

Q
progressed. These 3 species required a relatively deep substratum for burrowing and apparently a different food (ie., detritus) than the type used. Occasionally, unusually high mortality not associated with salinity appeared in some experi-mental containers but not in others. These mortalities occurred at all salinities and the causative agents apparently did not necessarily exert a synergistic effect at marginal salinities. On the other hand, after exposure to several different experi-mental salinities, some bivalves were capable of surviving more rapid changes in salinity than was possible immediately after collection. In effect, they had become ‘acclimated,’ and hence more resistant to physiological stress from salin-ity changes.
Differences in tolerance limits of the same species collected from different localities for this series of experiments most likely reflect seasonal differences in temperature, salinity and other environmental influences and probably are not due to the occurrence of physiolog-ically different races.
When bivalves survived in a given salinity, their activities were generally normal, except for some arcids and mytilids which apparently require higher salinities for byssus formation than for
other activities. Active species did burrow
and filter immediately after being moved
to salinities that eventually proved lethal.
However, there were no salinities at which
animals survived but did not burrow or

TABLE 31. Comparison of the minimum salinity necessary for survival of adults and for survival of larvae or reproduction.

Approximate
minimum salinity in %o
Species at which adult survives

Bankia gouldi 10
Crassostrea virginica 6
Gemma gemma 10
Mercenaria mercenaria 12.5
Mulinia lateralis 5
Mya arenaria 2.5
Mytilus edulis 8
Spisula solidissima 1255
Teredo navalis 6

Minimum salinity in %o
at which larvae survive
or reproduction occurs

10
5.6
10
15
Who
8 or lower
14
16
1.9

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filter.
There appears to be little difference in
the minimum salinity for survival of adult
bivalves and the minimum salinity for
reproduction and larval development
(Table 31). Data are available for only a few species but in only 1 case did the salinity tolerance limits for survival of adults or larvae and occurrence of reproduction differ by a maximum of 6%. Small bivalves frequently succumbed more rapidly to lethal salinities than did

larger individuals of the same species but there was no difference in the minimum salinity at which they would survive. Small bivalves adapted better to experimental conditions within their individual salinity tolerance range than the larger in-dividuals. This could be due to the stress of
overcrowding or increased metabolic
waste accumulation in the larger
specimens.
From the preceding discussion, it is
evident that the minimum salinity for

TABLE 32. Salinity tolerance limits of 36 species of bivalves as determined from natural distribu-tion and laboratory experiments.

Species Salinity range Experimentally determined
in nature in%o minimum salinity in %o

Argopecten irradians Above 15 15
Amygdalum papyria Above 10 7.5
Anadara ovalis Above 15 12:5
Anadara transversa Above 15 10
Anomia simplex Above 15 12.5
Bankia gouldi Above 10 =>
Barnea truncata Above 15 10
Brachidontes recurvus Above 5 4
Congeria leucophaeta Below 12 0
Crassostrea virginica Above 6 5
Cyrtopleura costata Above 10 5
Donax variabilis Above 30 12.5
Ensis directus Above 10 7.5
Gemma gemma Above 5 7.5
Laevicardium mortoni Above 15 7.5
Lucina multilineata Above 20 7.5
Lyonsia hyalina Above 15 7.5
Macoma balthica Above 5 2.5
Macoma phenax 2-20 2.5
Macoma tenta 20-30 a
Mercenaria mercenaria Above 12.5 12.5
Modiolus demissus Above 8 5
Mulinia lateralis Above 10 5
Mya arenaria Above 3 20
Mytilus edulis Above 8 ==
Noetia ponderosa Above 20 17.5
Nucula proxima Above 20 ==
Petricola pholadiformis Above 15 10
Polymesoda carolininana Below 15 ——
Rangia cuneata Below 15 0
Solemya velum Above 15 15
Spisula solidissima Above 28 12.5
Tagelus plebeius Above 10 2.5
Tellina agilis Above 18 12.5
Teredo navalis Above 6 ——
Yoldia limatula Above 20 ——

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oceanic salinities. D. variabilis, though
living on ocean beaches, undoubtedly
experiences some temporary reductions in
salinity after heavy rains. Juvenile S.
solidissima are frequently found on ocean
beaches and in estuarine waters but are found as adults only in deeper waters. In recent laboratory experiments juvenile Chama congregata, a species normally found only in oceanic water and not normally exposed to salinity reductions, were also discovered to be euryhaline. About 2/3 of the bivalves which occur in Virginia's estuarine and inshore environment occur naturally over the approximate salinity range they tolerated in the laboratory (Table 32). This would indicate ihat salinity is of prime importance in determining their distribu-tion. In Virginian waters, Mytilus edulis, Argopecten irradians, Macoma balthica and Mya arenaria are not commonly found over their entire salinity range though they are in other areas. Virginia is near the southern limit of the geographical range for both Mytilus edulis and Mya arenaria. As mentioned previously, summer water temperatures limit the distribution of Mytilus edulis to oceanic waters. Mya arenaria does not appear to be confined to low-salinity water by temperature. However, the unknown factor or factors which determine the southern range limit of Mya arenaria may serve to limit this species to intermediate and low-salinity areas within the coastal waters of Virginia. The bay scallop, Argopecten irradians is rare, and is restricted in Virginia to high-salinity water. Because this species is abundant both north and south of Virginia in a wider range of salinity, its distribu-tion along the coast of the state must be limited by other factors, for example, absence of suitable setting substratum or protective cover, formerly provided in the area by the extensive eel grass beds. Scallops were much more abundant prior to the disappearance of eel grass (Zostera marina) in the early 1930's. The absence of suitable habitat in the eastern shore bays may prevent scallop populations from recolonizing those areas of Chesapeake

Bay where salinity is above 15%o and eel grass, Rupia, or other suitable marine grass is established. In Virginia Macoma balthica is limited to low and intermediate salinity creeks with soft muddy substrata. This clam is found at higher salinities and in different substrata elsewhere. Biological competition for suitable habitats with 3 other tellinids (M. mitchelli, M. tenta, and Tellina agilis) may account for its distribu-tion in Virginia.
About 1/3 of the species studied have never been found naturally over the entire salinity range tolerated in the laboratory. Predation could cause this or perhaps this reflects a lack of adequate sampling in the cases of Tagelus plebeius, Laevicar-dium топот, Lyonsia hyalina, Barnea truncata, and Lucina multilineata. In other cases (Congeria leucophaeta, Rangia cuneata, Масота mitchelli, Donax variabilis, Тейта agilis, and Spisula solidissima), there can be no doubt that salinity is, by itself, not a major impor-tance in limiting distribution. In almost every instance, these species live in marginal habitats where species diversity, and therefore interspecific competition, is low. Congeria leucophaeta, Rangia cuneata and Macoma mitchelli are pri-marily brackish water forms that thrive at salinities too low for most marine bivalves and too high for fresh water bivalves. Donax variabilis inhabits the surf zone of ocean beaches where few other species of animals can survive. Tellina agilis and Spisula solidissima, though not living in unique habitats, may not inhabit their potential salinity range because of biological interaction such as predation or competition from other species, or special environmental requirements (i.e., high oxygen, low levels of suspended sediments, bottom type, etc.).
Tellina agilis and Macoma mitchelli are closely related species, virtually indistin-guishable except for their hinge structure. Both exhibited a wide salinity range in the laboratory (2.5-30%0) yet there is very little overlap in their distributions. М. mitchelli is found from 2-20% and T. agilis from 18-34% (Table 32). It again

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appears that some other environmental requirement determines their distribution. Spisula solidissima is adapted to the relatively stable oceanic environment which supports tremendous beds of this species. However, when larvae colonize inshore areas they rarely develop beyond the juvenile stage because they are subject to intense predation by a variety of crabs, carnivorous gastropods and bottom feeding fish. This predation rather than salinity prevents establish-ment of permanent populations of S. solidissima in estuarine areas.
The relationship, if any, between salin-ity tolerance and systematic position is not at all clear. In some taxonomic groups of closely related species, the separate species do not occur over the entire salinity range which the species can tolerate under experimental conditions. This could be due to interspecific competi-tion. Within the Mytilidae and Pholadidae, the species are separated by other environmental factors. For example, in the Mytilidae, Brachidontes recurvus is epibenthic and subtidal, Amygdalum papyria benthic intertidally and in shallow water. Modiolus demissus occurs high in the intertidal zone. In the Pholadidae Barnea truncata is found in peat, while Cyrtopleura costata is found in sand and soft mud.
In still another group, the Arcacea, closely related species coexist and inter-specific competition, if any, has no effect on salinity distribution. Anadara ovalis is found with both A. transversa and Noetia ponderosa. All 3 species of blood clams had relatively high salinity require-ments. There was no comparable taxonomic group with low salinity requirements.

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ZUSAMMENFASSUNG

SALZGEHALT-TOLERANZ EINIGER MEERESMUSCHELN VON
LANDNAHEN UND ASTUAR-BIOTOPEN IN DEN GEWASSERN VON VIRGINIA AN DER WESTKUSTE DES MITTELATLANTIK

M. Castagna und P. Chanley

Viele Arten Brackwasser-Muscheln haben eine Verbreitung, die eng mit dem Salzgehalt zusammenhangt, was die Wichtigkeit des Salzgehaltes fiir die Verbreitung zeigt. Die ungefáhre Amplitude der Salzgehalt-Toleranz fiir 36 Arten wird dargestellt. Die Toleranz-grenzen fiir 29 Arten wurden im Laboratorium experimentell bestimmt. Die meisten davon sind stark euryhalin. Alle blieben noch bei einem Mindest-Salzgehalt von 17.5% am Leben, und 25 Arten noch bei 12.5%. Zwanzig Arten ertrugen noch niedrigeren Salzgehalt.
Die Salzgehalt-Toleranz fiir ein und dieselbe Art ist nicht konstant sondern variiert mit der Jahreszeit, der Gewóhnung, der Temperatur. Eingraben, Nahrungsaufnahe und Vermehrung finden bei fast jedem Salzgehalt statt, bei dem die Art am Leben bleibt. Byssusbildung erfordert einen hóheren Salzgehalt, als er ftir andere Tatigkeiten nótig ist. In Virginia kónnen etwa zwei Drittel der besprochenen Salzwasser-muscheln in dem gesamten Salzgehaltis-Bereich gefunden werden, in dem sie im Laboratorium úberlebt haben. Elf Arten kommen nicht in ihrem gesamten móglichen Salzgehalt-Bereich vor. Acht davon, Yoldia limatula, Mytilus edulis, Venericardia tridentata, Lucina mul-tilineata, Dosinia discus, Abra aequalis, Mya arenaria, Martesia cuneiformis sind nahe der geographischen Grenze ihres Verbreitungsgebietes; ihre Verteilung kann lokal in erster Linie durch die Faktoren bestimmt sein, die ihre geographische Verbreitung bedingen. Die Verbreitung von 5 Arten, Argopecten irradians, Congeria leucophaeta, Macoma mitchelli, Donax variabilis und Spisula solidissima kann durch Feinde, Konkurrenz oder besondere ökologische Ansprüche beeinflusst werden. Vier von den 11

SALINITY TOLERANCE OF MARINE BIVALVES

Arten, Congeria leucophaeta, Macoma mitchelli, Donax variabilis, Rangia cuneata kommen an besonderen Biotopen mit geringer Arten-Mannigfaltigkeit vor.

HZ

RÉSUMÉ

TOLÉRANCE A LA SALINITÉ DE QUELQUES
BIVALVES MARINS DES MILIEUX LITTORAUX ET
D'ESTUARIES EN VIRGINIE, CÔTE OUEST MEDIO-ATLANTIQUE

M. Castagna et P. Chanley

Plusieurs bivalves d estuaires ont un type de distribution en corrélation avec la salinité, ce qui montre l'importance de celle-ci dans le déterminisme de leur distribution. Le niveau approximatif de tolérance saline pour 36 espèces de bivalves est décrit. La plupart de ces espèces montre un remarquable degré d'euryhalinité. Toutes survivent à une salinité minimale de 17,5% et 25 espèces survivent à 12,5 % . Vingt espèces survivent à diverses salinités plus faibles.
La tolérance saline pour une espèce donnée n'est pas constante, mais varie en fonction de la saison, du mode expérimental, de la température. Le fouissage, l'alimentation et la reproduction ont généralement lieu à presque toutes les salinités où la survie est possible. La formation du byssus réclame une salinité plus forte que celle nécessaire aux autres activités.
En Virginie, environ les 2/3 des espèces de bivalves étudiées peuvent être trouvées dans les limites de salinité qu'elles peuvent tolérer au laboratoire. Onze espèces ne se rencontrent pas jusqu'aux limites qu elles sont capables de supporter au laboratoire. Huit de ces 11 espèces, Yoldia limatula, Mytilus edulis, Venericardia tridentata, Lucina multilineata, Dosinia discus, Abra aequalis, Mya arenaria, Martesia cuneiformis, sont proches de leurs limites de répartition géographique. Leur distribution localement peut étre d abord limitée par les facteurs qui déterminent leur répartition géographique. La distribution de 5 especes, Argopecten irradians, Congeria leucophaeta, Macoma mitchelli, Donax variabilis, et Spisula solidissima, peut &tre influencée par la prédation, la compétition et des exigences spéciales d'environnement. Quatre de ces 11 espéces, Congeria leucophaeta, Macoma mitchelli, Donax variabilis, Rangia cuneata, se rencon-trent dans des habitats spéciaux de faible diversité spécifique.

AE

RESUMEN

TOLERANCIA DE SALINIDAD EN BIVALVOS MARINOS DE AGUAS COSTERAS Y AMBIENTES ESTUARINOS DE VIRGINIA

M. Castagna y P. Chanley

Muchas especies de bivalvos marinos tienen su distribución correlacionada a la salinidad, indicando la importancia de tal factor en los patrones distribucionales. Se estudiaron los limites de tolerancia en 36 especies; 29 fueron determinadas por experimentos de laboratorio. La mayoría muestran marcada eurihalinidad. Todas sobrevivieron a una salinidad minima de 17.5% y 25 а tan poca como 12.5% ; 20 sobrevivieron a concentraciones varias, menores.
La tolerancia de una especie dada no es constante sino que varia con la estación y la temperatura. Excavamiento, nutrición y reproducción ocurren a grado de salinidad en el que puedan sobrevivir, pero para la formación de biso requieren salinidades más altas.
En Virginia, dos terceras partes de los bivalvos discutidos se pueden encontrar entre los límites de salinidad que son capaces de resistir en el laboratorio. Once especies no aparecen en todos sus límites potenciales y ocho de las mismas, Yoldia limatula, Mytilus

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edulis, Venericardia tridentata, Lucina multilineata, Dosinia discus, Abra aequalis, Mya arenaria, Martesia cuneiformis, estan cerca del límite geográfico de tolerancia; sus distribuciones locales peuden ser limitadas, primariamente por los factores que deter-minan sus áreas geográficas. La distribución de cinco especies, Argopecten irradians, Congeria eucophaeta, Macoma mitchelli, Donax variabilis, y Spisula solidissima, pueden estar influenciadas por predación. Cuatro de las once especies, Congeria leucophaeta, Macoma mitchelli, Donax variabilis y Rangia cuneata, aparecen en habitats es-pecializados con diversidad de bajas salinidades.

ИТР:

АБСТРАКТ

ВЫНОСЛИВОСТЬ ПО ОТНОШЕНИК К СОЛЕНОСТИ НЕКОТОРЫХ МОРСКИХ BIVALVIA ИЗ ПРИБРЕЖНОЙ ЗОНЫ И ЭСТУАРИЕВ ВИРГИНИИ (ЗАПАЛНО-АТЛАНТИЧЕСКОЕ ПОБЕРЕЖЬЕ)

М. КАСТАНЬЯ И П. ЧЕНЛИ

Особенности распределения ряда видов Bivalvia тесно связано € распределением солености и имеет для них большое значение.
Описываются пределы выносливости различной солености 36 видов Bivalvia. ina 29 видов эти пределы были определены экспериментально. Большая часть изученных видов оказались очень оэвригалинными. Все моллюски выживали при наименьшей солености в 17.5°/oo, а 25 видов - при 12.507685; 20 видов выживали при различной, HO еще более низкой солености. Выносливость к солености данного вида не постоянна, а изменяется по сезонам, при опытах с соленостью и в зависимости от температуры. Закапывание, питание и размножение моллюсков обычно происходит почти при всякой солености, при которой только они могут выживать. Образование биссуса требует более высокой солености, чем другие виды елеятельности. В районе Виргинии около 2/3 исследованных морских двустворчатых моллюсков могут встречаться и при более высокой солености, чем та, которую они выносили в лаборатории. 11 видов не встречаются при солености, более высокой, чем та, которую они потенциально могут выдерживать. Восемь видов из одиннадцати - Yoldia limatula, Mytilus edulis, Venericardia tridentata, Lucina multilineata, Dosinia discus, Abra aequalis, Mya arenaria, Martesia cuneiformis находятся здесь почти на границе своего. географического распространения. Их местная встречаемость может ограничиваться прежде всего теми факторами, которые определяют их общее географическое распространение. На распространение пяти видов - Aequipecten irradians, Congeria leucophaeta, Масота mitchelli, Donax variabilis, Spisula solidissima могут влиять - хищники, кокуренция или особые потребности моллюсков в условиях обитания. Четыре из одиннадцати видов - Congeria leucophaeta, Macoma mitchelli, Donax variabilis, Rangia cuneata - встречаются в особых условиях обитания и при малом их видовом разнообразии.
Z.A.F.